

COMPETITION BETWEEN HARVESTER ANTS AND RODENTS IN THE COLD DESERT¹

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ABSTRACT.—Local distribution patterns of three rodent species (*Perognathus parvus*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*) were studied in areas of high and low densities of harvester ants (*Pogonomyrmex ouyheei*) in Raft River Valley, Idaho. Numbers of rodents were greatest in areas of high ant-density during May, but partially reduced in August; whereas, the trend was reversed in areas of low ant-density. Seed abundance was probably not the factor limiting changes in rodent populations, because seed densities of annual plants were always greater in areas of high ant-density. Differences in seasonal population distributions of rodents between areas of high and low ant-densities were probably due to interactions of seed availability, rodent energetics, and predation.

Competition for food is an important determinant of ecosystem structure and dynamics (Hairston et al. 1960, Brown and Davidson 1977), but, because the relative importance of competition as a determinant of community composition is debatable (Schoener 1974, Wiens 1977), additional study is essential to provide necessary insights into community relationships. Most studies of competition have dealt with interactions between species of closely related taxa (Connell 1961, Brown 1971, Sheppard 1971, Grant 1972, MacArthur 1972, Pianka 1974, Schroder and Rosenzweig 1975), but only recently have they included species of more distantly related taxa (Hansen and Ueckert 1970, Brown et al. 1975, Fenton and Fleming 1975, Primack and Howe 1975, Pulliam and Brand 1975, Sinclair 1975, Brown and Davidson 1977, Boyden 1978).

Although studies of harvester ants in North America have included distribution (Hull and Killough 1951, Sharp and Barr 1960, Cole 1968), damage and control (Cole 1932, Severin 1955, Lavigne 1966, Race 1966, Wight and Nicholes 1966), foraging activity (Cole 1934, Creighton 1953, Tevis 1958, Bernstein 1974, Rogers 1974, Whitford and Ettershank 1975, Whitford 1976), species diversity (Davidson 1977a, 1977b, Mares and Rosenzweig 1978), and taxonomy (Cole 1968), only a few studies in Arizona have examined com-

petition between ants and rodents (Brown et al. 1975, Pulliam and Brand 1975, Brown and Davidson 1977, Reichman, unpubl. ms.). Reichman (unpubl. ms) demonstrated that either taxon alone or both together impact the density of seeds in the soil, but Pulliam and Brand (1975) concluded that little competition exists between ants and rodents except in years of low seed production. Brown and Davidson (1977) concluded that ants and rodents do compete for seeds in southern hot deserts, and harvester ants can affect rodent distribution.

Our objective was to investigate local distribution patterns of rodents and ants to determine if competition for seeds was an important factor in any observed interaction between western harvester ants and rodents in the cold desert.

STUDY SITES AND METHODS

This study was conducted in a sagebrush-greasewood community at Raft River Valley, Idaho, from May through August 1977 and 1978. Predominant plant species were sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), squirreltail barley (*Sitanion hystrix*), and mustards (*Lepidium perfoliatum* and *Descurainia richardsonii*). Harvester ants were of the species *Pogono-*

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myrmex owyheei. Rodent species investigated were the white-footed deer mouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), and Great Basin pocket mouse (*Perognathus parvus*).

One 12 × 12 base grid with 15 m between stations, and 10 4 × 5 mini-grids with 10 m between stations were established to assess ant-rodent interactions. Approximately half of the base grid and five of the mini-grid were located in areas of high ant-density, but the remainder of the base grid and the other five mini-grids supported only low ant-densities.

Two Utah live traps (Garcia et al. 1974) baited with rolled oats were placed at each station on the base grid, which was trapped for 10 consecutive nights during May and August 1977 and 1978. The 10 mini-grids, with one Utah live trap at each station, were trapped simultaneously for four consecutive nights each month. Mini-grids were trapped prior to the base grid trapping in May and August. All animals on the base grid and mini-grids were marked for identification by clipping the toes and released after species, sex, and trap station were recorded. Numbers of rodents for the mini-grids and centers of activity on the base grid were estimated using Hayne's (1949a, 1949b) methods.

Understory vegetation (<30.5 cm high) and overstory vegetation (>30.5 cm high) were measured using the cover class and point quarter methods, respectively. Relative seed abundance and time of seed drop of annual forbes (*Descurainia richardsonii*, *Lepidium perfoliatum*) and grass (*Sitanion hystrix*) was determined monthly on the 10 mini-grids from soil samples, using the method of Franz et al. (1973).

In order to establish a relationship between distribution of *P. maniculatus* and seed abundance during the May reproductive period, sex ratios were calculated for specimens collected from the 10 mini-grids.

Ant mound volumes were used in conjunction with numbers of mounds per unit area to estimate ant density at each mini-grid (Fig. 1). Ant foraging activity was estimated twice each day during the first week of each month by placing a one-meter quadrat over each of 22 stations located 15 m apart in the

area of high ant-density of the main grid. Numbers of active ants/m²/minute were counted and averaged to obtain a monthly estimate of relative foraging activity. Seed preferences of harvester ants were determined on 23 June and 6 and 28 July 1978 for five mounds. Seeds were collected, identified, and counted from 75 returning foragers for each mound at each sampling period.

RESULTS

Areas of high ant-density had less total cover (32.8 percent and 42.2 percent in high and low ant-density areas, respectively) and less grass cover (0 and 32.7 percent in high and low ant-density areas, respectively) than did areas of low ant-density. Densities of seeds from annual plants (*Descurainia richardsonii*, *Lepidium perfoliatum*) were apparently dropped in late May and early June, whereas *Sitanion hystrix* seeds were dropped in July and August (Table 1). This temporal difference in seed drop was also reflected by the foraging activities of the ants (Table 2). In June, ants almost exclusively foraged on seeds from *D. richardsonii* and *L. perfoliatum*, whereas in July they foraged on *S. hystrix* (Table 2).

Ant foraging activity was lowest in May, peaked in July, and decreased in August (Table 3). There was a significant negative correlation ($p < 0.025$) between ant densities and rodent numbers (Fig. 2), but no significant correlation between rodent numbers and seed abundance ($p < 0.200$).

Average numbers of rodents in areas of low ant-density were 9 ± 3.2 rodents/grid in May and 16 ± 2.7 in August, an 88 percent increase; in areas of high ant-density the numbers of rodents were 26 ± 8.3 in May and 11 ± 2.7 in August, a 58 percent decrease (Table 4). Centers of rodent activity on the base grid shifted from the area of high ant-density to the area of low ant-density during August 1977 and 1978 (Table 4).

Sex ratios of *P. maniculatus* during the May reproductive period on the five mini-grids with low seed-density averaged 1.6:1 (1:1 to 2:1) males to females, and on the five grids with high seed-density they averaged 1:1.3 (5:11 to 13:8). When fitted to a binomial distribution these ratios were signifi-

cantly different ($p < 0.08$) in both high and low seed-density areas. The female-to-male sex ratios were also significantly greater ($p < 0.04$) in the areas of high seed-densities.

DISCUSSION

Studies of competition by Brown and Davidson (1977) between ants and rodents in Arizona indicate that seeds limit the distribution of either taxon, which also influences each other. Although they demonstrated significant evidence for exploitation competition between ants and rodents, our data from Idaho show that factors other than seed abundance are more influential in changing rodent distributions in areas of high ant-density. Our data indicate that *D. richardsonii* and *L. perfoliatum* seeds were always more abundant in areas of high ant-densities than

they were in areas of low ant-densities (Table 1). Because this condition persisted in spite of greater foraging pressure by ants and rodents, these seeds probably did not limit rodent populations or distribution. If seed of these species were not the limiting factor, then rodent populations should not have declined by 58 percent in areas of high ant-density. One might suspect an error in our data due to inappropriate sampling, but comparable results were obtained on the base grid. In August 1977 and 1978, significant shifts occurred in the centers of activity from the area of high ant-density to the area of low ant-density (Table 4). In fact, two *P. maniculatus* that established centers of activity in the area of high ant-density during May established new centers of activity in the area of low ant-density during August.

The negative correlation between ants and

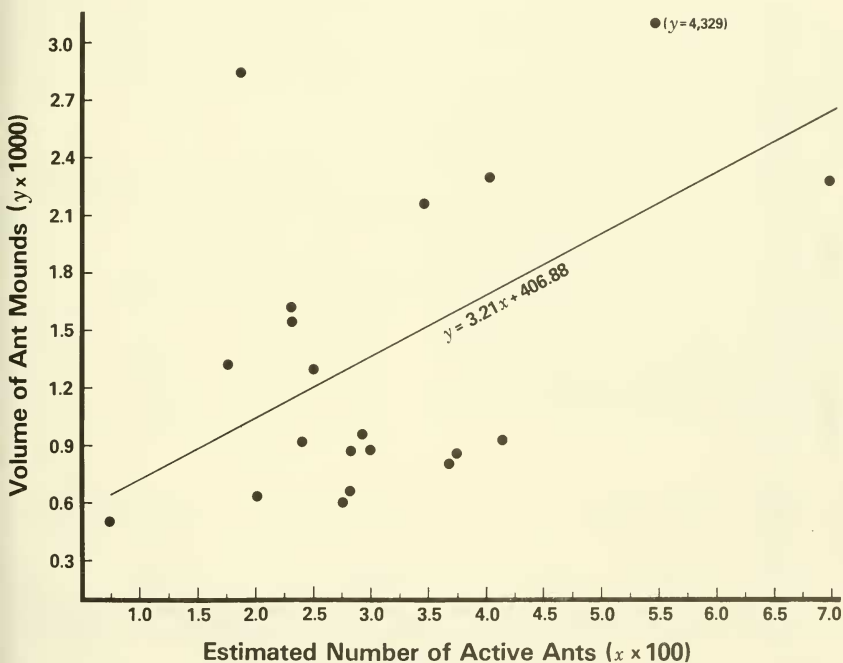


Fig. 1. Regression analysis of mound volume and estimated number of active ants ($p < 0.050$).

TABLE 1. Relative seed abundance and time of seed drop for *Descurainia richardsonii*, *Lepidium perfoliatum*, and *Sitanion hystrix* for May–August 1977.

Date	Annual seeds per sample			Grass seeds per sample		
	High ant-density	Low ant-density	Average	High ant-density	Low ant-density	Average
May	128	25	77	0	27	14
June	242	53	147	4	31	18
July	199	126	163	2	86	44
August	144	16	81	0	78	39
Average	179	55		3	56	

TABLE 2. Numbers and relative percentage of seeds from *Descurainia richardsonii*, *Lepidium perfoliatum* and *Sitanion hystrix* (grass) collected from 75 foraging ants at five ant mounds for the four sampling periods in 1978.

Date	Annual seeds	Grass seeds	Number combined	Percent of total	
				Annual seeds	Grass seeds
June 23	358	1	359	99.7	0.3
July 6	249	16	265	94.0	6.0
July 16	47	88	135	35.0	65.0
July 28	39	111	150	26.0	74.0



Fig. 2. The correlation between ant and rodent density ($p < 0.025$) is shown for May–August 1978.

rodents (Fig. 2), the 58 percent rodent population decline in areas of high ant-density (Table 3), and the shifts in rodent centers of activity (Table 4) indicate that interactions did occur between ants and rodents. Competition for seeds is probably not responsible for these interactions; consequently, other factors such as rodent energetics, predation, and seed availability may logically be expected to account for rodent distribution changes in areas of high ant-density. During the critical reproductive period in May, female rodents must secure sufficient energy for existence and successful rearing of young. At that time it seems critical that females be in areas of relatively high food abundance in order to maximize reproductive energy. Assuming this to be the case, two predictions can be generated: (1) rodent numbers will be higher in areas where seed abundance is greatest and (2) sex ratios will be weighted toward females in areas of high seed-density. Both of these predictions were realized in our studies. Areas of high seed-density were also the areas of highest ant densities (Table 1), but, because ants were inactive in May (Table 3), competition between ants and

rodents for seeds was nonexistent at that time.

Because of the temporal difference in seed drop between the annual herbaceous species (*D. richardsonii*, *L. perfoliatum*) and grass (*S. hystrix*), seeds from annual plants are more available in May and June, whereas the grass seeds are more available in July and August. This difference in seed availability was also reflected in the foraging activities of harvester ants. They foraged almost entirely on seeds from annual plants in June, but, as the season progressed and these seeds became less available due to ant-rodent foraging activities and the loss of seeds into soil crevices (Tevis 1958, Bernstein 1974), ants foraged primarily on grass seeds that were more available (Table 2). Since grasses were virtually nonexistent in areas of high ant-density (Table 1), rodents likely emmigrated to areas where those seeds were more abundant.

Rodents living in areas of high ant-density would probably be more susceptible to predators than those living in areas of low ant-density for two reasons: (1) areas of high ant-density have more open spaces and less total cover than areas of low ant-density (Table 1), (2) foraging time will increase as the seed availability of *D. richardsonii* and *L. perfoliatum* decrease. Observations in July and August indicated that predator pressure on rodents was greater in areas of high ant-density. Short-eared owls and burrowing owls were observed almost exclusively in those areas. Coyote signs were more abundant in areas of high ant-density, and the only weasel captured during the summer was on a grid with high ant-density. Because ecological theory suggests that small animals are more likely to be regulated by predation than competition (Hairston et al. 1960, Schoener 1974), our results suggest an alternative ex-

TABLE 3. Mean numbers \pm standard deviation of rodents/grid in areas of high and low ant-densities, and the relative ant-foraging activity for the period May-August 1978.

Date	Mean no. rodents/grid		Relative foraging activity
	High ant-density area	Low ant-density area	
May	26 \pm 8.3	9 \pm 3.2	8 \pm 12
June	29 \pm 6.2	24 \pm 4.3	56 \pm 30
July	17 \pm 4.1	18 \pm 2.8	104 \pm 70
August	11 \pm 2.7	16 \pm 2.7	26 \pm 13

TABLE 4. Distribution of centers of rodent activity for areas of high and low ant-densities on the base grid for May and August 1977 and 1978.

Rodent centers of activity	May			August		
	High ant-density area	Low ant-density area	Total	High ant-density area	Low ant-density area	Total
Number, 1977	16	27	43	3	12	15
Number, 1978	31	34	65	16	29	45
Percentage, 1977	37	63		20	80	
Percentage, 1978	48	52		35	65	

planation for observed ant-rodent distribution patterns to that proposed by Brown and Davidson (1977).

Differential predation pressure and seed availability are factors that have not been treated as complementary mechanisms influencing rodent distributions in areas of high ant-density. Although this is the first reported study of ant-rodent interactions in a cold desert, the results suggest that competition for seeds between the two taxa may not be as intense in cold deserts as indicated by Brown et al. (1975), Brown and Davidson (1977), and Reichman (unpubl. ms.) for the Sonoran Desert. Pulliam and Brand (1975) reported that competition for seeds between ants and rodents in the plains grassland region of Arizona may occur only in periods of drought. Because 1978 was an exceptional year for production of annuals (19.2 percent relative cover compared to 6.8 percent in 1977), active competition for seeds between the two taxa may have been masked.

Ants may exert a stronger influence on rodent distributions in cold desert environments than our data have shown. Because ants have an impact on the total vegetation cover of an area (Rogers and Lavigne 1974, Clark and Comanor 1975), their absence may allow increase in total shrub and grass cover, thus affecting rodent distributions. The decrease in availability of seed from annual plants probably would not be as dramatic if there were no ants present. If this were the case, then foraging time and consequent predation would not increase significantly as the season progressed. Further documentation of selection pressures such as predation and seed availability during drought years are needed before the extent of competition between ants and rodents in cold desert environments can be fully evaluated.

LITERATURE CITED

- BERNSTEIN, R. A. 1974. Seasonal food abundance and foraging activity in some desert ants. *Amer. Nat.* 108:490-498.
- BOYDEN, T. C. 1978. Territorial defense against hummingbirds and insects by tropical hummingbirds. *Condor* 80:216-221.
- BROWN, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. *Ecology* 52:305-311.
- BROWN, J. H., J. J. GROVER, D. W. DAVIDSON, AND G. A. LIEBERMAN. 1975. A preliminary study of seed predation in desert and montane habitats. *Ecology* 56:987-992.
- BROWN, J. H., AND D. W. DAVIDSON. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880-882.
- CLARK, W. H., AND P. L. COMANOR. 1975. Removal of annual plants from the desert ecosystem by western harvester ants, *Pogonomyrmex occidentalis*. *Environ. Ent.* 4:52-56.
- COLE, A. C. 1932. The relationship of the ant, *Pogonomyrmex occidentalis* Cresson, to its habitat. *Ohio J. Sci.* 32:133-146.
- . 1934. An ecological study of the ants of the southern desert shrub region of the United States. *Ann. Entomol. Soc. Amer.* 27:388-405.
- . 1968. *Pogonomyrmex* harvest ants: a study of the genus in North America. Univ. Tenn. Press, Knoxville. 222 p.
- CONNELL, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723.
- CREIGHTON, W. S. 1953. New data on the habits of the ants of the genus *Veronessor*. *Amer. Mus. Novit.* 1612:1-18.
- DAVIDSON, D. W. 1977a. Species diversity and community organization in desert seed-eating ants. *Ecology* 53:711-724.
- . 1977b. Foraging ecology and community organization in desert seed-eating ants. *Ecology* 58:725-737.
- FENTON, M. B., AND T. H. FLEMING. 1975. Ecological interactions between bats and nocturnal birds. *Biotropica* 8:104-110.
- FRANZ, C. E., O. J. REICHMAN, AND K. M. VAN DE GRAFF. 1973. Diets, food preferences, and reproductive cycles of some desert rodents. US/IBP/Desert Biome Research Memorandum RM 73-24 128 p.
- GARCIA, J. R., H. D. SMITH, AND C. D. JORGENSEN. 1974. A capture-release method for determining small mammal activity. *Proc. Utah Acad. of Sci. Arts and Letters.* 51:1-11.
- GRANT, P. R. 1972. Interspecific competition among rodents. *Ann. Rev. Ecol. & Syst.* 3:79-106.
- HAIRSTON, C. H., F. E. SMITH, AND L. B. SLOBODKIN. 1960. Community structure, population control, and competition. *Amer. Nat.* 94:421-425.
- HANSEN, R. M., AND D. M. UECKERT. 1970. Dietary similarity of some primary consumers. *Ecology* 51:640-648.
- HAYNE, D. W. 1949a. Calculation of size of home range. *J. Mamm.* 30:1-18.
- . 1949b. Two methods for estimating population from trapping records. *J. Mamm.* 30:399-411.
- HULL, A. C., JR., AND J. R. KILLOUGH. 1951. Ants are consuming Big Horn Basin ranges. Annual Livestock Review, Herdsman Edition, Sec. 2, Western Farm Life 53:70.
- LAVIGNE, R. J. 1966. Individual mound treatments for control of the western harvester ant, *Pogonomyrmex*

- mex occidentalis*, in Wyoming. J. Econ. Entom. 59:525-532.
- MARES, M. A., AND M. L. ROSENZWEIG. 1978. Granivory in North and South American deserts: rodents, birds and ants. Ecology 59:235-241.
- MACARTHUR, R. H. 1972. Geographical ecology. Harper & Row, New York. p. 111-207.
- PIANKA, E. R. 1974. Evolutionary ecology. Harper & Row, New York. p. 132-155.
- PRIMACK, R. B., AND H. F. HOWE. 1975. Interference competition between a hummingbird and skipper butterflies. Biotropica 7:55-58.
- PULLIAM, R. H., AND M. R. BRAND. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology 56:1158-1166.
- RACE, S. R. 1966. Control of western harvester ants on rangeland. N.M. Agric. Exp. Stn. Bull. 502. 21p.
- REICHMAN, O. J. 1979. Desert granivora foraging and its impact on seed densities and distributions (unpubl. ms).
- ROGERS, L. E. 1974. Foraging activity of the western harvester ant in the shortgrass plains ecosystem. Environ. Entom. 3:420-424.
- ROGERS, L. E., AND R. J. LAVIGNE. 1974. Environmental effects of western harvester ants (*Pogonomyrmex occidentalis*) on the short grass plains ecosystem. Environ. Entom. 3:994-997.
- SCHOENER, R. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.
- SCHRODER, G. D., AND M. S. ROSENZWEIG. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia 19:9-28.
- SEVERIN, H. C. 1955. Harvester ants and their control. S.D. Farm and Home Res. Winter 6:36-37.
- SHARP, L. A., AND W. F. BARR. 1960. Preliminary investigations of harvester ants on southern Idaho rangelands. J. Range Mgmt. 13:131-134.
- SHEPPARD, D. H. 1971. Competition between two chipmunk species (*Eutamias*). Ecology 52:320-329.
- SINCLAIR, A. R. E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. J. Anim. Ecol. 44:497-520.
- TEVIS, L., JR. 1958. Interrelations between the harvester ant, *Veromessor pergandei* (Mayr), and some desert ephemerals. Ecology 39:695-704.
- WHITFORD, W. G. 1976. Foraging behavior in Chihuahuan Desert harvest ants. Amer. Midl. Natur. 95:455-458.
- WHITFORD, W. G., AND G. ETTERS HANK. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. Environ. Entom. 4:689-696.
- WIENS, J. A. 1977. On competition and variable environments. Amer. Sci. 65:590-597.
- WIGHT, J. R., AND J. T. NICHOLS. 1966. Effects of harvester ants on production of a saltbush community. J. Range Mgmt. 19:68-71.